

## Chemical Communication in Insects<sup>1</sup>

May Inscoc

Organic Chemical Synthesis Laboratory, Agricultural Environmental Quality Institute, Beltsville Agricultural Research Center, ARS, USDA, Beltsville, Maryland 20705

### ABSTRACT

Many aspects of insect behavior are regulated by minute amounts of chemicals with highly specific action. Insects may use such compounds in finding mates, locating food or suitable sites of oviposition, recruiting workers, warning others of attack, and driving off enemies. As research on the nature and mode of action of these materials progresses, applications in insect pest management programs will increase.

Insects are greatly dependent on chemical signals throughout their lives. They find food and mates and suitable locations for oviposition by following chemical cues from other insects and from their surroundings. We can think of numerous examples. For instance, a column of ants carrying crumbs from a picnic table back to the ant hill is guided by the chemical trail laid down by the foraging ants that first discovered the food supply. When a swarm of honey bees, *Apis mellifera* L., is ready to move to a new nesting location, scouts are sent out first. When they return, the swarm subsequently follows these scouts to the new site, depending for guidance on chemicals the scouts give off. Unless the swarm senses the presence of the queen through her scent, however, many of the bees turn back (Morse, 1963). The presence of

a worker bee which has been treated with a queen bee extract fools the swarm enough that most of the bees will fly to the new site without a queen (Avitabile *et al.*, 1975); several different chemicals may be involved in this swarming behavior. Mosquitoes use chemical cues to find humans to bite and suitable waters for egg-laying. Perhaps the most dramatic examples of chemical communication are found in the various steps in insect mating. In this area the chemicals can be extremely effective in minute amounts. It has been reported that a single female introduced pine sawfly, *Diprion similis* (Hartig), in the five days of her adult life, was responsible for attracting the 11,000 males that were caught on the sticky board surrounding her cage (Coppel *et al.*, 1960).

It may be argued that such uses of chemical cues do not constitute communication in the strictest sense. Nevertheless, for want of a better term, "chemical communication" has become fairly standard usage. In a developing

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field of interest such as this, many terms are coined to convey specific meanings and those that are found useful by others eventually gain acceptance. "Semiochemical" is such a term, meaning a chemical that carries a message (Law and Regnier, 1971). Originally this term referred only to naturally-occurring substances, but chemicals from other sources are now often included.

Natural semiochemicals may be pheromones, allomones, or kairomones, three other recently-coined words. A *pheromone* (Karlson and Lüscher, 1959) is a substance secreted or emitted by one member of species that brings about a response in another member of the same species. The attractant emitted by that female sawfly I mentioned is a sex pheromone. Pheromones are intraspecific semiochemicals, acting within a species, affecting members of the same species. *Allomones* and *kairomones*, on the other hand, are transspecific (or interspecific); the emitter and the receiver belong to different species; transspecific semiochemicals have been called *allelochemicals* (Whittaker, 1970; Whittaker and Feeny, 1971). An *allomone* is "a chemical substance, produced or acquired by an organism, which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral or physiological reaction adaptively favorable to the emitter" (Brown, 1969). The reaction produced by a *kairomone* benefits the recipient of the message rather than the emitter (Brown *et al.*, 1970). Thus, the scent of a skunk would be considered an allomone, since it repels the skunk's enemies, while the rabbit odor that enables a fox to locate its prey is a kairomone, since the receiver (the fox) is benefitted by the message. These terms are not mutually exclusive. A bark beetle sex pheromone, frontalin, is used by some bark beetle predators to locate their prey (Vité and Williamson, 1970); thus, it is both a pheromone and a kairomone.

Insect hormones, which act internally within a single insect, do not fit into the scope of this discussion.

#### Examples of Non-Chemical Communication

I do not want to give the impression that all insect communication involves semiochemicals, for this is far from being the case. Chemicals are probably the most widely used means of insect communication, but many other methods are also known. Firefly lights, for example, can be mating signals. The males fly about, flashing in a pattern characteristic for their species, and females on the ground or on low perches flash answers back. A male receiving a correct answer to his flashed message, with the appropriate flash length and delay, comes closer and repeats his pattern. This dialogue continues until the male reaches the female. There is not always a happy ending, however, for some predatory females seem to have broken the code used by other species and have been observed to attract males of other species by mimicking the appropriate female response and then to devour the male when he gets within range (Lloyd, 1975).

Both a rat mite, *Laelaps echidnina* Berlese, (Bruce, 1974) and a bark beetle parasite (Richerson and Borden, 1972) have been reported to find their hosts by sensing the emitted infrared radiation.

Some planthoppers find their mates by means of vibrations. Females on a rice stem vibrate their abdomens, and males elsewhere on the plant sense the vibrations and respond if the frequency is right (Ichikawa *et al.*, 1975).

Some male cicadas attract females by their stridulation, or singing. This can be unfortunate for them, for one parasitic fly locates cicadas by means of this song, with the result that males are more frequently parasitized than females (Soper *et al.*, 1976).

Perhaps the best known non-chemical means of communication is the honey bee waggle dance which foraging workers use to inform other workers of the location of a food source. The straight-line portion of the dance pattern indicates the direction, while the waggle frequency shows the distance (von Frisch, 1946, 1974). Odors are also involved in relaying this information (Gould, 1975).

Many other examples of non-chemical means of communication could be cited, but that would be beyond the scope of this paper. My purpose is to outline some of the many roles semiochemicals play in the lives of insects and in their interactions with other insects and with their environment. More detailed information can be obtained from some of the numerous comprehensive reviews on various aspects of the subject, as, for example, Birch, 1974a; Eisner, 1970; Jacobson, 1972. Although a goodly number of these chemicals have been identified, many others are recognized only through their action. Our information in this area is far from complete.

#### Insect Olfaction

To receive the messages carried by these chemicals, insects must have some means of detecting them. Although a few pheromones seem to be detected by tasting, in most cases the detectors, or chemoreceptors, are found on the antennae (Schneider, 1974). Since it appears that the process of chemoreception by insect antennae is comparable to that whereby odors are detected by the human nose, the process is often referred to as insect olfaction (Schneider, 1969). Hopefully, studies of insect responses to semiochemicals will lead to increased understanding of how we detect and discriminate between various odors. Conversely, progress in mammalian olfaction and gustation may contribute to the understanding of insect chemoreception.

Studies of insect olfaction rely greatly on the electroantennogram (EAG) (Schneider, 1957), which is a measurement of the electrical response of an antenna to a chemical stimulus. EAGs have great utility in studies on the nature and mechanism of action of pheromones and in the identification of pheromonal components (Arn *et al.*, 1975).

Insects also have chemoreceptors that correspond to our taste buds, but gustation and general food attractants are not considered here.

Up to now, insect sex pheromones are the insect semiochemicals that have received the most intensive study. Naturalists have believed for a long time that scents were responsible for mate-finding by various moths. As long ago as 1690, for example, John Ray, a biologist, noted several male moths, *Biston betularia* (L.), fluttering around a cage in which a female of the species had just emerged from her chrysalis; in reporting this, he suggested that the scent of the female had attracted the males from outside (Mickel, 1973). Early collectors added rare specimens to their collections by using caged females as lures. The French naturalist Fabre (1900) published observations on various male moths attracted through open windows by caged female moths; one species of moth responding in this way had not been found in the area in twenty years.

By the early 1900's, then, it was well known that attractive materials given off by female moths of many species attract males and that these materials are very specific in their action. In moths, this material is usually produced by glands in the female abdominal tip, and females emitting the attractant lift the tips in a characteristic position referred to as "calling". The gypsy moth, *Lymantria dispar* (L.), is one insect that has received intensive study. Even in 1914, traps baited with live female gypsy moths were being used to locate new infestations of this forest defoliator and to delineate the extent of existing infestations (Collins and Potts, 1932). However, all females are not equally attractive, they live only a few days, and they are available for only a short time, so there are many factors limiting the utility of live female gypsy moth traps. In addition, there is always the possibility that a live female could escape and start a new infestation. By 1920 it had been found that extracts of female abdominal tips could be used in place of the live females, thus overcoming many of these ob-

stacles. The discovery in 1944 (Haller *et al.*, 1944) that hydrogenation of the extract increased its stability and attractiveness was another forward step. Nevertheless, without a knowledge of the chemical composition of the attractant, entomologists were dependent upon live insects to obtain the lure extracts for gypsy moth survey traps. The supply of these insects in the USA is very erratic; for several years, moths were collected in Spain to prepare extracts for USDA survey traps.

Widespread attempts at identifying the attractant pheromones of different insects continued, but it was not until 1959 that the identification of a sex pheromone, that of the silkworm moth, *Bombyx mori* (L.), was reported (Butenandt *et al.*, 1959). This accomplishment had required 20 years of careful experimentation, and half-a-million female pheromone glands were used. By an involved series of separation steps about 6 mg of pure substance was isolated from the extract of these glands. Microchemical studies (hydrogenation and permanganate oxidation) and synthesis showed this pheromone to be (*E,Z*)-10,12-hexadecadien-1-ol, called bombykol.

One requirement in pheromone identification studies is an adequate supply of insects, both as a source of pheromone and also as test subjects for use in following the isolation and purification steps. Butenandt and his group had insects readily available—silkworms have been “domesticated” for 4000 years at least. With other insects this has been a severe limitation. Unless a successful method for rearing has been developed, wild insects must be used and these may be available only for a limited time—sometimes not more than a week or two each year. Rearing insects is no easy task. Problems with diet and disease are but two of the many difficulties encountered.

Another requirement for successful pheromone identification is a good method of bioassay. Insects, like all living things, are extremely complex mix-

tures of chemicals, and to sort out the minute amount of unknown material from the relatively massive amounts of other similar and dissimilar chemicals, it is necessary to have some means of monitoring each step in a separation to locate the fraction containing the active material. The product of the pheromone gland of the female silkworm moth attracts males and causes intense excitation, with wing vibration and a circling sort of dance. Butenandt used the wing vibration in his bioassay, and his “unit of attraction” was defined on the basis of the concentration of material that would cause at least 50% of the males in a cage to start this vibration when a glass rod dipped into the solution was introduced. We now know that the attractive component (or components) in the pheromonal emission of a female moth is not necessarily the same as that causing stimulation, and the search for attractant pheromones cannot depend exclusively on a stimulatory response as a method of bioassay. The ultimate test of an attractant is a field test, and thus far there have been no reports of field tests with bombykol. After all, the silkworm is not a pest insect, so bombykol has not been needed for survey trapping, which is the means by which other pheromones have received the most extensive testing. It seems probable that bombykol is indeed an attractant as well as a stimulant, but this point needs clarification.

In the sixteen years since the discovery of bombykol was announced, many other attractant pheromones have been identified. This has been accomplished largely through advances in analytical methodology, such as microchemical techniques and instrumentation for chromatographic separations and spectrophotometric measurements. By now, more than 70 compounds have been identified as attractant pheromones, and several other compounds that are attractive seem to be pheromones but have not been rigorously proven to be present in the insect (Inscoc and Beroza, 1976).

Since the response of male moths to

“calling” females is generally very specific, it had been thought that attractant pheromones would be species—specific. This is not necessarily so. (*Z*)-11-Tetradecen-1-ol acetate, for example, has been identified in the attractant pheromone of 10 different moth species and is attractive in the field to males of 12 other species, making 22 species in all thus far. In 13 of these 22 species, another compound is also needed for maximum attractancy.

This requirement of more than one compound for attraction is rather typical of the complexities we are encountering as we learn more about the sex pheromones (Silverstein and Young, 1976). Very often, precise ratios of two or more components are found to be needed. With many moths that require two pheromonal components, the compounds are closely related chemically. For example, they may be opposite geometric isomers, differing only in the arrangement of atoms around a double bond (Beroza *et al.*, 1973a); positional isomers, having double bonds in different positions on the carbon chain (Meijer *et al.*, 1972; Tamaki *et al.*, 1971); homologues (Nesbitt *et al.*, 1975); or compounds with different functional groups, such as an alcohol and the corresponding acetate (Roelofs *et al.*, 1975), or an aldehyde and an acetate (Kochansky *et al.*, 1975b).

The European corn borer, *Ostrinia nubilalis* (Hübner), provides an interesting example. This insect was introduced into North America from Europe in broom corn shipments two or three different times between 1909 and 1914 and was first established in areas where brooms were manufactured. It spread fairly rapidly, though, and now it is a pest in most of the major corn-producing regions east of the Rocky Mountains. In the early 1970's scientists in Iowa reported that male moths responded to (*Z*)-11-tetradecen-1-ol acetate found in the female pheromonal emission and that the opposite isomer, (*E*)-11-tetradecen-1-ol acetate, inhibits this response; so that in the presence of more than 15% *E* isomer, no moths are attracted by the *Z* isomer (Klun and Robinson, 1971).

Despite this inhibition, it was soon found that small amounts (about 3%) of the *E* isomer are needed for attraction (Klun *et al.*, 1973). In New York, on the other hand, it was found that it is the *E* isomer that is attractive to the males and is the major component of the female pheromone (Roelofs and Comeau, 1971; Kochansky *et al.*, 1975a). Cooperative trapping studies (Klun and Cooperators, 1975) have recently shown that in most of Europe (Austria, Germany, Roumania, Poland, France, Spain, and Switzerland) and of North America (Iowa, Missouri, Minnesota, Nebraska, Georgia, Wisconsin, and several Canadian provinces), males respond to the *Z* isomer containing small amounts of the *E*, while in Italy, Netherlands, and New York, males prefer the other blend—*E* with a little *Z*. In Pennsylvania and New Jersey both kinds of response are found. This seems to indicate that the New York strain was brought to North America in a shipment from Italy and for some reason has not spread very far, while the major strain in North America came from elsewhere in Europe. Where the habitats of the two strains overlap, there seems to be practically no hybridization.

In addition to the attractant pheromones, other compounds may have a marked effect on the number of insects caught in attractant traps. I have already mentioned the inhibitory effect of large amounts of the minor isomer of the European corn borer pheromone. Other compounds drastically reduce trap catches of other insects, sometimes completely eliminating the attractancy even when present only in trace amounts. Compounds of this type have been called inhibitors or masking agents. Other compounds have been found that do not appear to be attractive in themselves but increase the effectiveness of a lure; these have been referred to as synergists. Compounds of both types have been found in pheromonal emissions.

Now we are finding that the terminology we have been using may be misleading (Kennedy, 1972). It is possible

that some of the compounds we consider attractant pheromones because they enable males coming from a distance to locate the females may not be attractants at all but may be acting as stimulants, activating the males to fly up-wind and search for the females; those that blunder into the traps in the course of their searching get caught. Other compounds seem to be true attractants, causing direct orientation to the source of emission. We are also finding that some of the so-called synergists do not act merely to increase the effectiveness of an attractant but play a definite role in the response of male moths, such as increasing the frequency of alighting (and thus increasing the probability of being caught in a trap) (Cardé *et al.*, 1975). Similarly, a compound that reduces trap catches when it is exposed in a trap with a lure and is therefore classed as an inhibitor may actually increase trap catches when disseminated over the surrounding area (Mitchell *et al.*, 1974; Rothschild, 1974). It is obvious that we know very little of how the sex pheromones work, and more behavioral studies are needed to clarify the function of various pheromone components and the point in the mating sequence at which each acts.

In most moth species that have been studied, the female attracts the male for mating. In fact, in some species the females have no wings (Tvermyr, 1969) and must rely completely on their attractant pheromone to bring males to them. Attractant pheromones may act over long distances. In one instance, a marked male moth was recaptured in a trap, baited with synthetic pheromone, 7.5 km from where he had been released the previous day (Kochansky *et al.*, 1975b). Lepidopteran attractants that have been identified thus far have been long-chain (10–18 carbon atoms) compounds of relatively simple structure, usually with one or two double bonds. Acetates are the compounds reported most frequently; numerous alcohols and aldehydes are also active. A ketone, (*Z*)-6-heneicosen-11-one (Smith *et al.*, 1975), a hydrocarbon, 2-methylheptadecane

(Roelofs and Cardé, 1971), and an epoxide, *cis*-7,8-epoxy-2-methyloctadecane (the gypsy moth pheromone, called *disparlure*) (Bierl *et al.*, 1970), have also been identified as lepidopteran pheromones. In insect orders other than the Lepidoptera, the situation seems more complex. Attractant pheromones are produced sometimes by the male, sometimes by the female, and a wide variety of structures have been found.

In the boll weevil, *Anthonomus grandis* Boheman (a coleopteran), for example, the male produces a pheromone that is attractive to females but that also attracts other males early and late in the season. It may therefore also be regarded as an aggregation pheromone, bringing insects of both sexes together. Four components, all having cyclic structures, have been identified, and some combination of at least three of these is necessary for attraction (Tumlinson *et al.*, 1969).

Bark beetles, which are very destructive in evergreen forests, also emit aggregating pheromones (Borden, 1974). In various species of *Dendroctonus*, in which the male is monogamous, a female finding a suitable tree starts boring a mating chamber and emits a pheromone, which, in combination with volatile materials from the tree, is very attractive to males, as well as being an aggregating pheromone (Renwick and Vité, 1969; Wood, 1970). In *Ips* spp. the polygamous male is the one that starts boring into the tree and gives off a pheromone advertising for mates as well as attracting other males to attack the tree (Wood, 1970). This is a great oversimplification, for bark beetles of both sexes emit a variety of pheromones.

The sex pheromones I have mentioned thus far have served to bring insects together for mating. Other sex pheromones may act to make the female more receptive. Some male butterflies have complex glands ("brushes" or "hairpencils") that are the source of aphrodisiac pheromones that release mating behavior in the female (Birch, 1974b). Male queen butterflies, *Danaus gilippus berenice* (Cramer), brush "hairpencil dust" onto

flying females to induce them to alight (Pliske and Eisner, 1969). Certain male cockroaches give off "seducin," a volatile substance that has not been identified, which induces the female to feed on a liquid oozing from the male tergal glands and makes her receptive to mating (Roth and Dateo, 1966).

#### Trail Pheromones

Pheromones other than sex pheromones are also known and are particularly important in the lives of social insects. Among these are the trail pheromones, which are used by ant or termite foragers returning to the nest with food. Ants heading home extrude their sting and deposit streaks of chemical on the path. Other workers following the trail reinforce it as long as food is found, but workers returning empty-handed no longer deposit the pheromone and the trail soon fades away. Ants will follow an artificial trail drawn with contents of the pheromone gland from a single ant and mill around in confusion at the end of the trail (Wilson, 1963). Up to now, very few trail pheromones have been isolated and identified, although many insects have been shown to use such pheromones. Of the ten compounds that have been reported, six are used by one ant species; these are fatty acids with 6 to 12 carbon atoms (Huwyler *et al.*, 1973). The other four known trail compounds are an alcohol, (*Z,Z,E*)-3,6,8-dodecatrien-1-ol (Matsumara *et al.*, 1968), an ester, methyl 4-methylpyrrole-2-carboxylate (attalure) (Tumlinson *et al.*, 1972), a macrocyclic hydrocarbon, 12-isopropenyl-1,5,9-trimethyl-1,5,9-cyclotetradecatriene (Birch *et al.*, 1972), and a heterocyclic compound, 3-butyl-octahydro-5-methylindolizine (Ritter *et al.*, 1973). All together, four ant and eight termite species have been found to use one or another of these ten compounds.

#### Alarm Pheromones

These trail pheromones recruit workers for food-gathering. Other pheromones may recruit for defense; some of

the alarm pheromones have this function (Wilson, 1975b). Alarm pheromones (alerting pheromones) are wide-spread in the social insects and elicit a variety of responses, such as excitement, flight, attraction, and attack. Probably more of these compounds have been identified than of any other type of pheromone, but in many cases the function of the individual compounds has not been elucidated, and all the components found in an alarm secretion may not necessarily be pheromones. Like most trail pheromones, alarm pheromones are short-lasting in their effects and act only over short distances. These properties are reflected in their molecular size. To act rapidly and be dissipated equally rapidly, these compounds must be relatively volatile, and most alarm pheromones have molecular weights between 100 and 200 (Wilson, 1970), with 5-12 carbon atoms; they include hydrocarbons, ketones, aldehydes, and esters. There is much less species specificity in alarm pheromones than in other pheromones and sometimes several species respond to the same alarm pheromone. This is not surprising, for a threat to one insect often threatens others also. Unlike other pheromones, which are usually present only in trace amounts, alarm pheromones are often present in fairly high concentrations.

Responses to alarm pheromones are many and varied. Often insects are attracted by low concentrations. At higher concentrations, response is related in large part to the organization of the colony. With semisocial insects such as the bed bug, *Cimex lectularius* L., (Levinson *et al.*, 1974) or with ants that live in small, loosely-organized colonies (Regnier and Wilson, 1969) in places like rotting logs, the alarm pheromones act as an early warning signal for evacuation and they scatter in all directions. These insects are not well-equipped for defense, and flight is the only practical strategy for them. For other ants in tightly organized colonies, increasing concentrations of the alarm pheromone stimulate the insects to attack. The red

harvester ant, *Pogonomyrmex barbatus* (F. Smith), is one of these. Workers of this species will attack a wad of cotton treated with 4-methyl-3-heptanone, a component of its alarm pheromone, and when a small drop of this compound was placed on one of the ants, it was immediately chased and attacked by near-by nest mates (McGurk *et al.*, 1966). Longer exposure to this pheromone brings on still another reaction, that of digging and carrying away pebbles. It has been suggested, but not proven, that this is because the pheromone also acts as a signal to rescue nest mates buried in a cave-in.

The pheromones I have discussed so far—sex pheromones, trail pheromones, and alarm pheromones—are the ones with which we are most familiar, but pheromones with many other actions are known.

#### Miscellaneous Pheromones

There are oviposition pheromones, for example. Some mosquito larvae give off a substance stimulating oviposition by the adult females (Kalpage and Brust, 1973). The advantage of this is clear; a location where eggs have successfully hatched has proven its suitability, while an untried pool may be only temporary and may dry up before eggs laid there can hatch. This pheromone would be an example of an oviposition-stimulating pheromone. Oviposition-deterrent pheromones are also known. After laying an egg, female black cherry fruit flies, *Rhagoletis fausta* (Osten Sacken), or apple maggot flies, *Rhagoletis pomonella* (Walsh), drag their ovipositors about the fruit and deposit a substance that discourages other females from laying in the same fruit (Prokopy, 1972, 1975). Some parasitic wasps similarly mark host eggs or larvae in which they have laid eggs (Vinson and Guillot, 1972; Guillot *et al.*, 1974). By preventing over-parasitization, this gives the parasite larvae a chance to develop without competition.

The mixture of fatty acids given off by some dead ants can also be regarded

as a pheromone (Wilson *et al.*, 1958). These fatty acids act as a signal to the workers to carry the dead ant out of the nest and put it onto the refuse pile. A live ant that has been daubed with some of these chemicals receives exactly the same treatment. No matter how often it returns to its nest, it gets carried back to the dump; the process is repeated over and over, and the hapless ant isn't allowed to remain in its nest until the "odor of death" finally wears off.

Other pheromones are involved in nest and colony recognition (Hubbard, 1974), brood tending (Glancey *et al.*, 1970; Bigley and Vinson, 1975), thermoregulation (Ishay, 1972), and a host of other phases of insect life.

There is even evidence for a "cannibalism pheromone" that causes diploid honey bee larvae to be eaten by the workers (Dietz and Lovins, 1975). The pheromones considered thus far have all been "releaser" pheromones—they bring about an immediate release of some action in the receiver. Another group of pheromones are the "primer" pheromones that trigger a physiological change in the receiving insect. The result of such a change is particularly noticeable in the desert locust, *Schistocerca gregaria* (Forskål), and other locusts. In dry years these insects resemble ordinary green grasshoppers and tend to remain solitary, poking around for food by themselves. The rains of wet years, however, stimulate hatching of eggs in large numbers, and it seems (Gillett, 1975; Nolte *et al.*, 1973) that a gregarization pheromone excreted by the young hoppers accumulates in large enough quantities to stimulate a color change from green to yellow and black and a change in habit from preferring a solitary existence to becoming part of a devastating swarm. Among other primer pheromones are ones that control caste changes in termites (Lüscher, 1961; Nagin, 1972) or prevent development of a new queen bee as long as there is an active queen in the hive (Butler *et al.*, 1961). Some of the various functions of pheromones are summarized in Table I.



Table I.—Insect pheromones.

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Sex Pheromones
Attractants
Inhibitors
Stimulants
Aphrodisiacs
Aggregation Pheromones
Trail Pheromones
Alarm Pheromones
Others
Oviposition stimulant
Oviposition deterrent
Territorial marking
Brood tending
Necrophoric
Colony recognition
Thermoregulation
Caste determination
Inhibition of queen rearing

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#### Allelochemicals

Up to this point we have been considering pheromones—chemicals used by insects for communication with other members of their own species. Insects also employ other semiochemicals, the allomones and the kairomones. With these materials, communication is interspecific—between members of different species. It should be remembered that these classifications are for convenience and are not exclusive. A pheromone can also be an allomone or a kairomone.

#### Allomones

Allomones, by definition, are interspecific semiochemicals that evoke a reaction that benefits the emitting organism in some way. By way of illustration, let us consider some slave-maker ants. At least thirty-five species of ant are known to depend to some extent on slave labor by other ants (Wilson, 1975a). Slave-maker workers raid a nest of another species and capture worker pupae, which they carry back to their own nest. When adults emerge from these captured pupae, they accept their new home and instinctively carry on the necessary housekeeping tasks—foraging for food, tidying the nest, and caring for the eggs and larvae of their captors. Some slave-makers rely on brute force in their raids and kill resisting workers to capture the

pupae they are after. A few species have been found to be more subtle. Workers of *Formica subintegra* Emery and *F. pergandei* Emery have enlarged glands that contain relatively enormous amounts (up to 10% of the entire body weight) of three esters—decyl acetate, dodecyl acetate, and tetradecyl acetate (Regnier and Wilson, 1971). These compounds are effective alarm pheromones. A small amount of an applicator stick poked into the edge of a nest of this species caused the entire colony to become highly excited and attracted most of the workers, who tried to attack the stick. These same esters also cause alarm in the nests of ants that are used as slaves. In this case, however, the result is panic; when the raider ants discharge these compounds, the excited workers run about aimlessly and scatter in all directions, leaving the nest free for the raiders to get the pupae they are seeking. The scattered ants do not return to their nest, probably because the odors of these esters, which are less volatile than most alarm substances, remain around the area for a long time. These three esters, then, act both as alarm pheromones, summoning raiding workers to the attack, and also as allomones, producing a reaction of panic in the attacked species that aids the attackers.

Many of the defensive secretions used by insects for their protection can be regarded as allomones. These secretions, which an insect emits when it is disturbed, to protect itself from predators, come in many forms—a fine spray or jet, a slow ooze, or even a foam (Eisner, 1970). A great variety of chemicals have been identified as defensive compounds (Weatherston and Percy, 1970), including aliphatic acids, esters, aldehydes, ketones, hydrocarbons, quinones, steroids, and terpenoid compounds. Most defensive secretions contain several different compounds; analysis of the secretion from a tenebrionid beetle showed the presence of more than fifty compounds (Tschinkel, 1975). Some compounds are irritants or repellents, others are distasteful to attackers, and others appear

to make the secretion more effective by increasing spreading or penetration. (Venoms and other toxicants from insect stings or bites are not generally classed as defensive secretions.) Defensive materials may act as repellents or irritants, or they may set up into a sticky material that interferes with the predator's actions. Some bombardier beetles use a reaction much like that involved in an aerosol can of hot shaving lather (Ane-shansley *et al.*, 1969). A hydroquinone reacts with hydrogen peroxide and the hot reaction products are sprayed out as a fine mist that reaches temperatures of 100°C. The benzoquinones in the reaction mixture are strong irritants, so the result is both chemical and thermal heat. A well-known defensive secretion is formic acid, which gets its name from its occurrence in a number of formicine ants, where it was first reported (though mis-identified) in 1670 (Wray, 1670). It is found in many insect species; in some it may also serve as an alarm pheromone. Many other alarm secretions are also defensive secretions, rallying attackers as well as acting as a repellent to invaders.

Some predators have learned to circumvent the defensive spray of their insect prey. Grasshopper mice have been observed to subdue beetles that spray irritating quinones from a gland in the abdominal tip by holding them head-up so all the secretion is ejected onto the ground (Eisner *et al.*, 1963). The mouse can then eat the beetle with impunity.

The defensive spray of some insects contains hydrocarbons such as undecane that may function by interfering with chemoreceptors on the predators' antennae (Blum and Brand, 1972). Insects often rely on their antennae to locate their prey, and if the prey insect can disable these antennae, it has a good change of getting away.

A defensive chemical need not be aimed at the predator directly. A Brazilian wasp suspends its small paper nest by a narrow stem, 2-3 cm. long. Wasp larvae are very attractive to ants, but the adult wasps smear the suspending stem

of the nest with a repellent substance that foraging ants will not pass (Jeanne, 1970). With this protective barrier, the larvae are safe in the nest, and the adults need not leave a wasp on guard while they are away.

Although the viscous or sticky materials in defensive secretions might be regarded as being a mechanical rather than a chemical defense, the repellent and irritant components are clearly allomones; they are chemicals conveying a message that is of benefit to the emitter.

Flower scents may attract insects in search of nectar. In gathering the nectar, the insect picks up pollen, which it then brushes off onto other flowers. The flower scents are therefore allomones, because the action elicited by the scent results in pollination of the flowers. Some Mediterranean orchids have a different twist (Kullenberg, 1961, 1973). Their scent appears to contain some of the same compounds that are in the female sex pheromone of certain wasps. The flowers themselves look enough like wasps to fool males attracted and stimulated by the scent, and in attempting to mate, the males are brushed by the pollinia and unwittingly act as pollen carriers.

#### Kairomones

Unlike the allomones, kairomones carry a message that results in benefit to the receiver of the message, rather than the emitter. Often these are scents used by parasites or predators to find suitable prey (Vinson, 1976). Relatively few insect kairomones have been identified thus far; these include a number of hydrocarbons that stimulate host-seeking behavior by various parasites of the corn earworm, *Heliothis zea* (Boddie) (Jones *et al.*, 1971, 1973). Heptanoic acid in the frass from potato tuberworm, *Phthorimaea operculella* (Zeller), larvae is another; it elicits heightened searching behavior by a parasitic wasp (Hendry *et al.*, 1973).

Lactic acid in human sweat is one of the cues used by some mosquitoes to locate someone to bite (Acree *et al.*,

1968). It therefore would also be considered a kairomone.

Codling moth, *Laspeyresia pomonella* (L.), larvae are attracted by a substance found in apple skins,  $\alpha$ -farnesene (3,7,11-trimethyl - 1,3,6,10 - dodecatetraene) (Sutherland and Hutchins, 1972). This same compound stimulates oviposition by adult female codling moths (Wearing and Hutchins, 1973). Thus, it seems to ensure that eggs are laid where the hatching larvae will find suitable food. Other oviposition stimulants in plants are known. Allyl isothiocyanate, found in cabbages and similar plants, stimulates oviposition by some insects (Gupta and Thorsteinson, 1960; Traynier, 1965). Certain glucosides from olives stimulate oviposition by the olive fruit fly, *Dacus oleae* (Gmelin) (Girolami *et al.*, 1975), but if the olives are damaged, a substance in the olive juice acts as a repellent, thus preventing eggs from being laid where chances of hatching are reduced. The glucosides can stimulate the females to lay eggs in molded paper mounds where they are easily accessible; they may thus simplify mass rearing of the fly.

Another substance of plant origin, not yet identified, aids a larval parasite of the artichoke plume moth, *Platyptilia carduidactyla* (Riley), (Bragg, 1974) in locating its host. A substance in the sap of artichoke plants that have fresh wounds such as might be made by the moth larvae attracts this parasitic wasp and stimulates it in its search for its larval host. This material illustrates again the overlapping that may be encountered in classification. Since the artichoke plants are benefitted by parasitization of the larvae feeding on them, the material is an allomone. On the other hand, it aids a parasite in locating its prey and acts as a kairomone.

Polyphemus moths, *Antheraea polyphemus* (Cramer), will not mate unless oak leaves are present. The reason for this puzzling observation was traced to a volatile compound, (*E*)-2-hexenal, given off by the leaves (Riddiford, 1967). Female moths will not "call" and release

their attractant pheromone in the absence of this compound, and males will not mate unless the females "call". Accordingly, there is no mating unless suitable larval food is available in the form of oak leaves. (*E*)-2-Hexenal is therefore a kairomone. Interestingly, this aldehyde is found in the defensive secretions of a number of insects; in the secretion of some cockroaches, the compound is sufficiently pure to induce moth mating even in the absence of oak leaves (Riddiford, 1967).

Up to this point I have given a brief run-down on a few of the myriad ways in which chemicals are involved in the interaction of insects with their surroundings. In interactions between insects and man, man often comes out the loser. Insects are often vectors of disease. Besides being painful, some insect stings can cause dangerous allergic reactions. Insects can destroy valuable trees, make damaging inroads on farmers' crops, and consume a large portion of the harvest when it is in storage. To cut down on insect depredations, man uses a varied arsenal of weapons, among which are the semiochemicals. As we reduce our reliance on pesticides, we will have to rely more on alternative methods of control and find new ways of using non-toxic chemicals such as these chemical messengers.

#### Synthetic Materials

One approach has been to search for effective repellents and attractants by empirical screening of chemicals (Beroza, 1970). A large number of compounds are tested for activity; other compounds related to those showing some activity are then synthesized and tested. By following leads in this way, we eventually may come across a compound with sufficient activity to have practical applications. Deet, *N,N*-diethyl-*m*-toluamide, the most effective repellent for mosquitoes and biting flies that we have up to now, was found in this way (McCabe *et al.*, 1954). Effective attractants for a number of insects, including the

Japanese beetle, *Popillia japonica* Newman (McGovern *et al.*, 1970), the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Beroza *et al.*, 1961), and some yellowjacket wasps (Davis *et al.*, 1972), have also been developed by this route. These synthetic attractants do not occur naturally in the insects, although methyl eugenol, the oriental fruit fly, *Dacus dorsalis* Hendel, attractant (Steiner, 1952), has been found in some leaves and flowers (Kawano, 1968; Fletcher *et al.*, 1975). Concentrations of these synthetic lures that are needed for attraction are much greater than those for the attractant pheromones. For example, traps for the Mediterranean fruit fly are usually baited with over a gram of trimedlure (*tert*-butyl 4(or 5)-chloro-2-methylcyclohexanecarboxylate) (Howell *et al.*, 1975), while amounts of the gypsy moth pheromone used in survey traps have ranged from 10  $\mu$ g to 10 mg, and traps baited with 1 ng of this pheromone have caught moths even after 3 months exposure (Beroza *et al.*, 1971).

#### Applications

As we have seen, chemicals that affect insect behavior at many stages in their development are now known, and as analytical methodology improves, additional compounds are being reported with increasing frequency. The question now is, "How can we use these compounds?"

An obvious use of attractants is in traps, which I have mentioned already. Baited with attractant pheromones or synthetic lures, these have become an indispensable tool in surveys to locate new insect infestations, to estimate the size of existing infestations, to determine the most effective timing for application of control measures, and to check on the effectiveness of these controls. Last year, for example, 17,000 traps baited with attractants for three fruit flies were deployed around various southern ports of entry to guard against importation of these flies. Last fall a few Mediterranean fruit flies were found in these traps in one county in California (Anon., 1975),

and control measures were quickly initiated to prevent the spread of the incipient infestation. Thousands of other traps for the gypsy moth, the Japanese beetle, pink bollworm, *Pectinophora gossypiella* (Saunders), and other insects are being used similarly in surveys for these pests.

Design of an effective trap is a research project in itself (e.g., Kennedy, 1975). Each insect has its own behavioral idiosyncracies that must be taken into account. Factors such as trap color, trap height, trap shape, size and position of trap entrance, and location of lure must all be considered. The trapping agents may be mechanical baffles or sticky materials that prevent escape, water or another liquid that drowns the insects, a toxicant, or an electrocutor grid. All in all, traps come in a bewildering array of sizes and shapes.

Theoretically, it should be possible to control small insect infestations by putting out traps in sufficient numbers. Up to now, however, this has not proved practical. With the sex attractant traps, for example, only adults, and only those of one sex, are caught. (Boll weevil pheromone traps are exceptions, since the sex pheromone also acts as an aggregation pheromone and males as well as females are trapped.) Since it is usually the larvae that do the damage to the crops, reliance on these traps for immediate crop protection would be something like locking the barn door after the horse had been stolen. Nevertheless, trapping of adults will cause a reduction in the next generation, provided that there is no migration into the area. Promising results have been obtained in some trapping tests (e.g., Beroza *et al.*, 1973b; Trammel *et al.*, 1974) and mass trapping may eventually develop into a feasible procedure. Tests are now underway with several insects.

A related application is the use of pheromones to attract insects to insecticide-treated trap crop plots; this procedure was effective in tests against the boll weevil (Scott *et al.*, 1974; Hardee *et al.*, 1975).

At the present it appears that mating

disruption by general dissemination of a sex pheromone throughout an area will be developed into a practical means of control more rapidly than trapping methods. Results in tests with a number of insects have been promising (e.g., Beroza, 1976; Roelofs *et al.*, 1976; Shorey *et al.*, 1976; Tumlinson *et al.*, 1976; Rothschild, 1975). Last summer, for example, a microencapsulated formulation of the gypsy moth pheromone was sprayed over 75 square miles in northeastern Maryland at a rate of 6 g/acre, with the result that mating of female gypsy moths was reduced by about 70% in the treated area. The mechanism behind such mating disruption is not yet clear. Perhaps the pervasive pheromone overloads the chemoreceptors in the males' antennae so that they no longer detect the females' pheromone; perhaps the concentration of the synthetic pheromone is high enough to mask the odor trails leading to individual females. It is quite possible that different mechanisms may be involved with different species. Pheromones affecting other phases of the mating process may be even more effective than the attractant pheromones with some insects, and in some cases compounds that are not pheromones may also act as mating disruptants. Air permeation with attractant inhibitors has disrupted mating of the European corn borer (Klun *et al.*, 1975) and the redbanded leafroller, *Argyrotaenia velutinana* (Walker), but dissemination of inhibitors has been ineffective with several other insects. This is an area where we have much to learn.

Trapping and mating disruption are but two potential applications of pheromones. As our knowledge increases, we should expect to find other ways of manipulating insects with their own chemical communication systems. For example, the aphid alarm pheromone,  $\beta$ -farnesene (7,11-dimethyl-3-methylene-1,6,10-dodecatriene), which is given off when an aphid is attacked, causes other aphids feeding nearby to drop off the plants as a way of rapid escape; it has been suggested that this behavior might be utilized for aphid control (Bowers

*et al.*, 1972). Another type of pheromone with potential utility for insect management is the oviposition marking pheromone that deters repeated oviposition (Prokopy, 1972; Yamamoto, 1975); field application of partially purified pheromone produced by female *Rhagoletis cerasi* (L.) reduced infestation of treated cherries by nearly 80% (Katsoyannos and Boller, 1976). The brood-tending pheromone of the imported fire ant, *Solenopsis invicta* Buren, is still another prospect for use in control. Filter paper discs treated with the pheromone were rapidly carried into the nest by workers and treated as pupae; the pheromone may thus provide a means of introducing and localizing insecticide treatments within a colony (Bigley and Vinson, 1975).

Applications of other semiochemicals are also being explored. Release of parasitic wasps is proving to be one way of reducing corn earworm, *Heliothis zea* (Boddie) populations; in small field tests, distribution of kairomones of the corn earworm that stimulate host searching by *Trichogramma* spp. resulted in more even distribution of the released parasites and less dispersal away from the treated area (Lewis *et al.*, 1975; Jones *et al.*, 1976).

From all appearances, semiochemicals will prove to be most effective in combination with other methods of insect control. Attractants may be used to bring insects to an area where they can be killed with a toxicant or treated with a pathogen or a chemosterilant. Destruction of palm trees in Samoa was reduced by infecting the coconut rhinoceros beetle, *Oryctes rhinoceros* (L.) population with a virus with the aid of traps baited with a synthetic lure (P. A. Maddison, personal communication), and some beetles infesting granaries have been inoculated with a protozoan infection by means of a pheromone-baited device (Schwalbe *et al.*, 1974).

A pilot test against the boll weevil has demonstrated the potential of integrated insect management through coordination of various suppression techniques, including the use of pheromones

(Hedin *et al.*, 1976). Late season insecticide treatments were used to reduce overwintering weevil populations. Removal of cotton plants after harvest destroyed food and shelter to cut down chances of survival of weevils that escaped the insecticide. Pheromone traps were used for monitoring throughout the test and were set out in the spring to catch emerging weevils. The release of male weevils treated with a chemosterilant dealt the final blow by ensuring that any surviving females would produce only infertile eggs. Despite some migration of weevils into the treated area from infested fields outside, the two-year program effectively eliminated the weevil from two-thirds of the experimental area.

As we learn more about insect semiochemicals and their behavioral effects, we can expect to find many new and imaginative ways of using them in insect management programs.

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